The evolution and frequency of female color morphs in Holarctic Odonata: why are male-like females typically the minority?

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Abstract

We compiled data on the occurrence and frequency of distinct female variants among Holarctic Odonata and interpreted the data in light of harassment-based hypotheses. The major source of male confusion for male mimicry hypotheses is predicted to be signal similarity between andromorphs and male distractors; for the learned mate recognition hypothesis (LMR), it is predicted to be variation in female signals. Mapping morphism state onto molecular phylogenies of *Ischnura* and *Enallagma* failed to resolve the general ancestral female condition. However, it appeared that the andromorphic state may be ancestral in one case, and that blue structural colors were ancestral to orange and green pigmentations. Of the poly-morphic species surveyed, 13% had more than two morphs, 4% had multiple heteromorphs but no andromorph, and 7% of 'monomorphic' congeners were functionally polymorphic because developmental variants mate. Such female signal variation lies beyond the scope of simple male mimicry, but nevertheless should exacerbate a male's problem in searching for mates. Andromorphs were the majo-rity morph in at least some populations of 17% of the species for which data were available. Andromorph frequencies of *Enallagma* species were generally higher than in *Ischnura* species, as expected if *Ischnura* andromorphs have higher signal apparency. Andromorph frequency varied significantly across habitats and species, as expected if per capita harassment and signal apparency vary among habitats. Quantification of signal apparency and per capita harassment across populations and among species is required to more rigorously test the extent to which variati-on in signal crypsis can explain observed variation in morph frequencies.

Introduction

Male-specific variation in color pattern or behavior has generally been explained in terms of alternative male mating tactics (Gross 1996). In contrast, little research has focused on how females avoid sexual harassment, here defined as unwanted

sexual attention. Such harassment towards females often carries fitness costs (e.g. Rowe et al. 1994; Holland & Rice 2001; Sirot & Brockman 2001). In the Odonata, female-specific color polymorphism is thought to be an evolutionary response by females to sexual conflict of interest over mating that favors males mating more often than is optimal for female fitness (see Fincke 1997). If that is the case, then the widespread occurrence of female-specific polymorphisms found in the Odonata offers an excellent opportunity to understand how sexual conflict or mutual benefit, as distinct from sexual selection per se, could lead to sexual dimorphism and spur rapid speciation (Fincke 2004).

A single autosomal locus with multiple alleles has a major effect on the variation in female body coloration and pattern. The male-like andromorph is the homozygous recessive state in *Ischnura damula*, *I. demorsa* and *Ceriagrion tenellum* (Johnson 1964, 1966; Andrés & Cordero 1999). The heteromorph, which differs from males in color and pattern (Johnson 1975) is the recessive case in *I. graellsii* and *I. elegans* (Cordero 1990; Sánchez-Guillén et al. 2005). However, gene-environment interactions greatly expand the range of phenotypic variation that can be attributed to genes alone. Some of the latter, such as temperature-induced changes in *Argia* (May 1976) that occur in both sexes are not considered in this paper. More generally, however, females may express a distinct developmental morph (e.g. Fincke 1987; Robinson & Jordan 1996, van Gossum et al. 2001a) or changes in hue over the course of a day or season that cannot be attributed to genetic change (T. Schultz and O. Fincke unpubl.). We here propose that female polymorphism can be considered 'genetic' when there are two or more heritable color morphs, but we designate 'functional polymorphism' when genetically monomorphic females mate while in color states that change with age or physiological state and hence may affect a male's behavior. By making this distinction, we stress that functionally, color variation may generate different visual signals irrespective of origin.

Harassment hypotheses and signal detection

Comparative data from North American and European Odonata offered tentative support for an anti-harassment function of female color polymorphisms (Fincke 2004). Female-specific variation was non-randomly distributed among families, occurring more often in species whose males search for potential mates than in resource-defense territorial species, where unreceptive single females can avoid mate-seeking males by staying clear of oviposition areas. Within several genera, the polymorphism occurred more often in species described as common or locally abundant than in rare ones, as expected if the latter experience lower per capita sexual harassment relative to the former. While offering support to the general hypothesis that the color polymorphisms function to reduce sexual harassment, these trends do not distinguish among current hypotheses for the maintenance of this female variation.

Viewed in the context of a signal detection problem (see Duda & Hart 1973), an odonate male that searches for receptive females in a noisy visual environment must distinguish the signals of a potential mate from those of undesirable 'dis-

tractor' individuals. The degree to which conspecifics of both sexes and morphs act as signal distractors should be a function of the chromatic and behavioral vector distance between them (Fig. 1). In *Enallagma*, a male's saturated colors reflect dominant wavelengths of ambient light and contrast strongly with natural background. For both the blue and orange *Enallagma* clades, male coloration is most conspicuous at the time and locations at which males are active (T. Schultz unpubl.). Sherratt & Forbes (2001) proposed that the colors of *Enallagma* males serve as conspicuous signals of sexual identity that reduce male-male harassment. Males might also benefit by offering a conspicuous signal to females in need of sperm, especially in low-density populations. In either case, by extension, the male-like andromorphs may often be more visually conspicuous than heteromorphs. Their relatively greater conspicuousness may reduce some of the advantage gained by their greater signal similarity with males (Fincke 2004), a possibility that has not previously been appreciated in the discussion of the evolution of female color polymorphisms.

The more intuitive notion is that their conspicuous signal makes male-like females more susceptible to visual predators (e.g. Robertson 1985; Hinnekint 1987). Nevertheless, differential rates of predation on morphs, either above or below water, that lead to morph-specific differences in survivorship have yet to be documented. Spectrally, the color of many heteromorphs closely matches natural backgrounds where females forage and oviposit (T. Schultz unpubl.), but many predators of polymorphic damselflies cue more to movement than color (Fincke 1994). Van Gossum et al. (2004) found spider predation was greater on males and heteromorphs than on andromorphic female; they also found heteromorphs moved more than andromorphs but did not determine whether andromorphs consequently had longer lifespans.
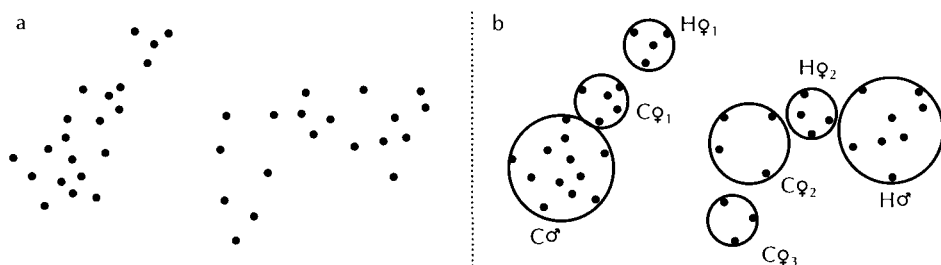

Figure 1: Signal detection problem for a male zygopteran that must distinguish between 'desired' signals of conspecific females and 'distractor' signals of conspecific males and heterospecifics of both sexes. Statistically differentiated clouds are signals, scatter of points around the center of each represents noise, distance between the center of two signals is *d*, the vector distance, a measure of signal similarity — (a) unsupervised learning; (b) supervised learning with identifying tags (see Duda & Hart 1973). Mimicry hypotheses assume that a male has an innate 'tag' by which to identify heteromorphs ($C\female_2$, $C\female_3$), but no such 'tag' for the andromorph ($C\female_1$). In contrast, the LMR hypothesis assumes that males have a more general innate 'tag' for 'female' and that a male learns to distinguish among the possible signals. – C: conspecific; H: heterospecific.

Mimicry hypotheses and relevant predictions

Harassment-based hypotheses can be classified according to the predicted nature of the female response to harassment, and consequently, the problem that the evolutionary response by females poses to males. A suite of male mimicry hypotheses assume that whereas the heteromorph is always recognized as a 'female', the male-like andromorph functions as a male mimic, which is invariably more difficult for males to recognize as 'female', either by heterospecific (Johnson 1975) or conspecific males (Robertson 1985; Hinnekint 1987; Sherratt 2001). Under that scenario, the ancestral state should be the heteromorphic one from which andromorphs diverged in response to increasing sexual harassment. Support for this view comes from some *Ischnura* species whose andromorphs very closely resemble males in color patterns and behavior, in which a male's sexual reaction towards live andromorphs was found to be statistically indistinguishable from that towards males (Robertson 1985; Andrés et al. 2002; Sirot et al. 2003). Nevertheless, when female behavior was restricted, Gorb (1999) found that male *I. elegans* responded sexually more often to andromorphs than to conspecific males or the duller heteromorphs. This suggests that the andromorph may have greater signal apparency with regard to coloration and pattern, providing them with a higher signal to noise ratio. In *Enallagma* and *Coenagrion*, all females have a sex-specific dark abdominal dorsum, which cues their sex to males (Gorb 1998; Miller & Fincke 1999). When presented with alternative individuals, males reacted sexually to females of either morph more than they did towards other males (Miller & Fincke 1999, 2004; O. Fincke and A. Fargevieille unpubl).

Morph-specific costs such as greater predation on andromorphs are required for both Johnson's (1975) proposed reproductive isolation benefit and Robertson's (1985) proposed benefit that andromorphs mate relatively less frequently than heteromorphs. However, several studies of lifetime reproductive success on marked individuals in three genera of coenagrionids (Fincke 1982, 1986, 1994; Thompson 1989; Cordero et al. 1998) found that morphs did not differ in their mating rates or survivorship. Similarly, while andromorph frequency and mating rates increased with population density (Cordero et al. 1998; Van Gossum et al. 1999), mating rates rose proportionately for all morph types, contrary to Hinnekint's (1987) density-dependent hypothesis (but see Cordero et al. 1998). Hence, among the male mimicry hypotheses, Sherratt's (2001) signal detection model appears to be the most viable. Like all of the mimicry-based hypotheses, Sherratt's (2001) model considers only a female's signal similarity with male distractors as a source of male confusion and requires that males innately recognize heteromorphs as 'female'. Sherratt's model predicts that andromorph frequency should rise with the operational sex ratio (OSR). As male/andromorph frequency rises, males are predicted to learn to detect andromorphs as potential mates. Comparisons of andromorph frequency among populations of four species indicated no correlation between andromorph frequency and OSR, contrary to Sherratt's prediction (McKee et al. 2005). Because his model lacks any component of frequency-dependent selection on heteromorphs, Sherratt predicted a posteriori that male preference for andromorphs could be equal to, but not exceed, male preference for heteromorphs. Contrary to that prediction, in a population of *E. boreale* in which andromorphs accounted for the majority morph, males exhibited a sexual preference for andromorphs (Forbes 1994).

Learned mate recognition hypothesis and relevant predictions

In contrast with all of the above mimicry-based hypotheses, the negative frequency-dependent selection model of learned mate recognition (LMR, Miller & Fincke 1999; see also Fincke 1994) focuses on signal variation among females as the primary source of a male's confusion. Males are expected to increase their searching efficiency by cueing to the morph detected most recently, exerting negative frequency-dependent selection on all female variants that mate, analogous to apostatic detection of variable prey by visual predators. Harassment costs to the majority type should be reflected in decreased fecundity due to time lost to harassment and possibly additional matings, although the latter isn't critical. Such harassment may come from conspecifics but also from congeneric species whose females are similar in color and pattern. Differential fecundity among morphs would be expected in non-equilibrium populations. At equilibrium, morph fitness, but not necessarily morph frequency, should be equal (Fincke 2004). The LMR hypothesis enjoys empirical support from experiments demonstrating that males develop a temporary sensory bias towards the morph type experienced most recently (*Enallagma*, Miller & Fincke 1999; O. Fincke & A. Fargevieille unpubl.; *Ischnura*, Van Gossum et al. 2001b), and that male harassment towards morphs is frequency dependent (Van Gossum et al. 2001c). A population genetics model demonstrated that negative frequency-dependent selection can maintain three morph types in the population indefinitely (Svensson et al. 2005). Contrary to the underlying assumption that heteromorphs are innately more readily recognized as 'female', experiments with naïve males indicated they have no innate preference for either morph type (O. Fincke and A. Fargevieille unpubl.). The latter study also indicated that males had no innate preference for conspecific females over either morph of a sister species.

Because it assumes signal variation is the primary source of a male's confusion, the LMR hypothesis is consistent with either morph type being ancestral, although the sexually monomorphic condition (andromorphic state) would seem to be the most parsimonious scenario. The LMR hypothesis predicts that more than two morphs should occur when the presence of a third lowers per capita harassment, without accruing any cost to a female of being overlooked (Fincke 2004). Developmental color change such as that which occurs in many *Ischnura* species should function as an additional female variant, particularly when such females mate (e.g. Van Gossum et al. 2001a; Sirot et al. 2003). If males learn to recognize females, then signal similarity with multiple distractors such as males or congeneric females of either morph should increase a male's confusion. Additionally, other factors contribute to signal crypsis (see Staddon & Gendron 1983), and hence, to a male's detection problem. A low signal aspect may result because the signal hue is similar to that of the background, and/or because of low signal brightness (Endler 1992). Signal apparency, the inverse of crypsis, may vary across a species range and depend on when and where species are active.

The LMR hypothesis, which is consistent with either morph type as the majority morph, predicts that morph frequencies should become more equitable with rising per capita harassment. Morph frequency should vary across populations and species as a function of signal apparency and per capita harassment rate. The latter is expected to be correlated with population density. Asymmetry in signal apparency should shift predicted morph frequencies away from equality at equilibrium, independent of population density or OSR (Fincke 2004).

Role of signal apparency in determining morph frequencies under negative frequency-dependent selection

In species whose andromorphs most closely resemble bright males, the andromorph signal should have the highest signal:noise ratio. In *Enallagma* species, andromorphs often appear less bright than the males and may be less conspicuous against background vegetation than the bright andromorphs of some *Ischnura* species or of *Ceriagrion tenellum* (Table 1). At equilibrium, when harassment rates towards morphs should be equal, the lowest andromorph frequencies should be found in species with the highest signal apparency. The difficulty, of course, is that we don't know how signal similarity and signal:noise ratio, which affect the general apparency of a signal, are integrated in the perceptual physiology of male damselflies. The equilibrium frequency should be that at which the ease of learning a morph type is balanced by its actual or effective rarity. Females can behaviorally modify their accessibility to males (reviewed by Fincke 1997). The fewer encounters a male has with a female variant, the harder it should be for a male to learn to recognize that female type. Note that females may differ in their physiological response to harassment, as is suggested by results from Sirot & Brockman (2001). If harassment costs are differentially incurred under natural conditions (e.g. Van Gossum et al. 2004), the predicted equilibrium frequency may differ from that predicted by visually cued harassment alone.

Here, we document morph state, frequency of the genetic morphs when known, and presence of developmental color variants in the polymorphic genera of Holarctic Odonata. We use the data to map color state onto current molecular and morphological phylogenies and to assess how consistent the LMR and mimicry hypotheses with respect to observed morph frequencies and types.

Table 1. Factors affecting signal apparency and their predicted relative values for two hypothesized classes of species. Both background noise and signal similarity (the inverse of d_{male}, the vector distance between the female and male signals), affect signal apparency. To the extent that a noisy visual environment is more confusing to males than signal similarity, the more conspicuous morph should be the minority morph. Andromorphs (A) may often be the minority morph, if they have higher general signal apparency relative to heteromorphs (H).

	Morph type	Signal/noise	Signal similarity
Ischnura-like species	A	High	High
	H	Low	Low
Enallagma-like species	A	Moderate	Moderate
	H	Low	Low

METHODS

We quantified the distribution of multiple female variants in odonates from North America, excluding Mexico (Walker 1953, 1958; Dunkle 1989, 1990, 2000; Westfall & May 1996; Manolis 2003, Acorn 2004; Lam 2004), Europe (Schmidt 1929; Hammond & Merritt 1985; Peters 1987; Askew 1988; d'Aguilar & Dommanget 1998; Brooks & Lewington 1999; Sternberg & Buchwald 1999, 2000), and temperate Asia (Sugimura et al. 2001) by first consulting the above identification guides. Additionally, we used data from published species accounts, monographs, unpublished field notes, personal collections and photos from reliable sources. Many of the latter are available on the worldwide web. In cases of discrepancies, we gave preference to accounts of authors who paid particular attention to live females in field populations (e.g. Dunkle 1990, 2000; Lam 2004) over those who did not focus on such variation (e.g. Nikula et al. 2003) or relied on descriptions based on dried, faded specimens (e.g. Westfall & May 1996; M. May pers. comm.). Whenever possible, we communicated with experts to achieve consensus.

To determine the ancestral state and extent to which phylogeny may constrain the evolution of morph states within genera, female character states (i.e. polymorphic, andromorphic, or heteromorphic) were mapped onto the molecular phylogeny of *Enallagma* species (Turgeon et al. 2005, using mtDNA gene COII) and *Ischnura* species (Chippendale et al. 1999, using mtDNA gene COII, rDNA 12S, and cytochrome b). These were the only groups for which detailed molecular phylogenies were available. The *Enallagma* phylogeny includes most of the Holarctic species whereas the *Ischnura* phylogeny includes only 15 of the 27 (56%) *Ischnura* species treated in this paper. To view the relationship between polymorphic and monomorphic families more broadly, we used the phylogeny by Rehn (2003), which is based on morphological characters. Although Turgeon et al. (2005) recognized *E. risi* and *E. vernale* Gloyd as species, we treated the former as a subspecies (see Samraoui et al. 2002), but did not include the latter, due to the current reservations about its specific status, in our data set; scoring them as separate species did not change any of our conclusions.

We scored a species as female polymorphic if it was known to have at least one population with stable body or wing color variants of mating females. For several *Enallagma* species, female polymorphism could be inferred from the description by a single author, but photos and illustrations by other authors, plus our own experience and the collection of D. Paulson suggested otherwise. Then, we conservatively scored such species as monomorphic (e.g. *pallidum* and *traviatum*). We scored more than two morphs when the female color variation appeared to be sufficiently disjunct to distinguish it from more continuous color variation such as exists within many *Enallagma* heteromorphs that vary from brown to green. In some *Enallagma* species, the pale tan and gray colors of immature female heteromorphs and andromorphs, respectively, are unsaturated versions of the mature form, whereas in genera such as *Ischnura*, these 'juvenile' morphs exhibit saturated colors that are distinct from the color of older sexually mature females. Some species, such as *I. kellicotti*, have been classed as polymorphic when in fact they represent age variation (Robinson & Jordan 1996) and are only functionally polymorphic. Hence, to determine the extent of such functional polymorphism, we scored distinct ontogenetic morphs, and whether such females were known to mate with males.

We ignored changes such as those occuring in *Libellula depressa, L. fulva, Orthe-trum cancellatum, O. coerulescens, Sympetrum striolatum* and *S. sanguineum* when old females change to a more male-like color (Sternberg & Buchwald 2000). Despite what may be functional polymorphism, those species don't exhibit multiple female variants. Also ignored were temperature-induced, reversible color changes as occur in some *Argia* and *Aeshna* species (May 1976; Sternberg 1996). These temporary changes occur in both sexes, and hence likely function in context other than sexual harassment. Finally, we excluded polymorphism based on structural elements (e.g. *Ischnura*, Schmidt 1967; Haritonov 1988), which are not charac-teristic of color polymorphic species more generally. We noted andromorph frequency and locality if sample sizes were ≥ 20. Data from collections typically provided pooled frequencies for a given geographic area rather than a specific population. With the exception of the few cases in which the statistics had already been done (McKee et al. 2005; Sánchez-Guillén et al. 2005), we used χ^2 tests to determine whether reported morph frequencies differed significantly across one or more populations of the same species. Frequencies that did not differ from equality were not used to assess when andromorphs were the majority morph. We used *t*-tests to determine frequency differences between *Enallagma* and *Ischnura* species. In the two primary mate-searching families Coenagrionidae and Aeshnidae, in genera with more than one polymorphic species we also noted the morph state of all monomorphic congeners. We did this for all North American and European spe-cies; Asian species were included when well known. We designated monomorphic species 'andromorphic' if the females were similar to the conspecific male in colora-tion, even though the color might be less intense than in the male, and the black patterns may differ (e.g. *Enallagma, Coenagrion* mentioned above). Lacking spec-tral reflectance data on males and females, in many species, especially anisopterans, the designation for monomorphic species was admittedly somewhat subjective; females often had an intermediate blend of male-like patterns and colors.

  We could not resolve all discrepancies among authors, in part because the degree to which andromorphs resemble males differed among clades. *Enallagma* andro-morphs all differed somewhat from the males in the color and melanin patterning; immature females, heteromorphs, and andromorphs differed from each other in hue but not in pattern. In contrast, andromorphs of *Ischnura* more closely match the pigmentation pattern of males, and differ distinctly from heteromorphic females in pattern. More problematic, however, were cases in which the signal variation was more continuous than distinct. For example, it was especially difficult to categorize the *E. signatum* clade, a group of species that develop green, yellow, orange or red pigmentary colors after a blue juvenile phase expressed in both males and females. In species with red males, the females exhibit paler yellow colors which we scored as functional heteromorphs. In species with yellow or orange males, reproductive females display continuous variation in color from blue through green to the color of the male. These color variants may represent females at different stages of post-teneral color development rather than ranges of reaction of discrete genetic morphs. The blue *signatum* females maintain their blue color much longer than the males, and mate in the blue state (Tennessen 1975). We classified such species as functionally polymorphic. Note that in contrast to other *Enallagma* species, blue females in this clade constitute heteromorphs while andro-morphs were difficult to classify because they exhibit male-like pigmentation to

different degrees. We designated *signatum*, *pollutum*, *sulcatum*, and *vespersum* as monomorphic andromorphs primarily to distinguish them from *concisum*, *dubium*, and *pictum*, whose females spectrally cluster more distantly from males (T. Schultz unpubl.).

Ischnura females show very complex variation, best understood by how they cluster into developmental groups. Many *Ischnura* species are presumably genetically polymorphic. In the North American group represented by *barberi*, *capreolus*, *cervula*, *damula*, *denticollis*, *erratica*, *gemina* and *ramburii*, heteromorphic females are typically orange or yellow when immature and duller brownish when mature, whereas andromorphs are colored very much like the male. In another group of *Ischnura*, heteromorphs are similar to those of the first group, but the sexually mature andromorphs express the male-like color pattern only briefly. With age, the andromorphs become pruinescent and indistinguishable from pruinose heteromorphs. This pattern is represented by *demorsa* (Johnson 1966), *perparva* (Paulson 1999) and *verticalis* (Fincke 1987). In still another group, no andromorph has been detected: *hastata*, *posita*, and *prognata*. Finally, *I. kellicotti* is monomorphically andromorphic. Orange *kellicotti* females become blue as they mature, and finally become pruinose. We scored *kellicotti* as functionally polymorphic. Some Eurasian *Ischnura* species are among the most complex, with at least five functional morphs (*elegans* and *graellsii*, Cordero 1992; Jödicke 1996; *genei*, B. Kunz pers. comm.).

RESULTS

Table 2 indicates the 144 Holarctic polymorphic taxa (in 134 spp.) known to occur, the range of andromorph frequency across populations as known, presence of a developmental morph type and whether the latter is known to mate. The female type of the 61 monomorphic congeners of Holarctic Coenagrionidae and Aeshnidae is listed in Table 3. In this table, the dichotomous terms 'andromorph' and 'heteromorph' are used only for convenience. As mentioned below, in some cases, females exhibited continuous variation in phenotype between unequivocal andromorphs and heteromorphs and therefore did not easily fit into such designations.

Mapping morph types onto a phylogeny based on family characters indicated that the polymorphism had evolved independently at least three times (Fig. 2). Within the current molecular phylogenies of North American *Enallagma* and *Ischnura*, polymorphism with the existence of an andromorph appeared to be ancestral (Fig. 3). The andromorphic state was possibly ancestral in the case of *E. exsulans*. Of the polymorphic species, 13% had more than two morph types whereas 4% were polymorphic but lacked a female morph that resembled the conspecific male (i.e. *Argia cuprea*, *lugens*, *moesta*, *oenea*, and *tibialis*). For example, in *A. moesta*, whose males have a whitish thorax, and *A. tibialis*, whose males are violet, the blue female morph was more similar to male *A. apicalis* than to conspecific males. Developmental color morphs occurred in 12% of the polymorphic species and in 23% of the monomorphic congeners surveyed. They were nearly ubiquitous in *Ischnura* but also occurred in *Enallagma*. Of the 134 polymorphic species, 6% had functionally more than two morphs because females in both the juvenile and mature color stages mated with males, whereas 7% of the species scored as monomorphic were functionally polymorphic because the developmental morph was known to mate.

Table 2. Holarctic Odonata with color polymorphic females — D: distribution – H: Holarctic, N: Ne-arctic, P: Palaearctic; – Region: refers to the region where the frequency has been judged. – Frequency: of andromorphs, with *n* in brackets; ranges refer to different populations; data from different years for same site are entered on separate lines; — E: existing, R: rare, Min: minority, Maj: majority. – Note that females with a post-reproductive pruinosity (e.g. several *Orthetrum* spp.) or with a general switch to a heteromorphic (e.g. *Nehalennia speciosa*) or male-like coloration (e.g. *Anax imperator*) during maturity are not considered in that context. Asterisked frequencies are from collection data pooled across multiple sites. [+] refers to a review with too much data across years to include here.

Taxon	D	Region	Frequency	Source
Zygoptera: Calopterygidae: *Calopteryx*				
splendens ancilla Selys [1]	P	Poland	R	Selys (1854); Fudakowski (1932); Jödicke (1999)
s. balcanica Fudakowski [1]	P	W Balkans	Maj	Fudakowski (1930); Adamovic & Vijatov (1996)
		W Greece	Min	Stobbe (1990)
		Albania	Min	Dumont et al. (1993)
s. caprai Conci [1]	P	Italy	0.10 (151)	de Marchi (1990)
s. faivrei Lacroix [1]	P	W France	Min	Lacroix (1915, 1919)
s. intermedia Selys [1]	P	Turkey	ca 0.5	Dumont (1977)
		Iran	Maj	Schmidt (1954)
s. johanseni Belyshev [1]	P	Siberia	E	Belyshev (1955)
s. mingrelica Selys [1]	P	Greece	Min	Stobbe (1990)
Lestidae: *Lestes*				
sponsa (Hansemann)	P	Europe	R	Schmidt (1929); Jödicke (1997)
		Kanto and Shikoku, Japan	Maj	Sugimura et al. (2001)
Coenagrionidae: *Argia*				
alberta Kennedy	N	N America	0.25 (20)*	D. Paulson (unpubl.)
apicalis (Say)	N	OK, USA	0.48 (115)	Bick & Bick (1965)
		N America	0.49 (35)*	D. Paulson (unpubl.)
barrettii Calvert	N	N America	E	Westfall & May (1996)
cuprea (Hagen) [2]	N	N America	E	D. Paulson (unpubl.)
emma Kennedy	N	N America	E	D. Paulson (unpubl.)
extranea Hagen	N	N America	0.24 (21)*	D. Paulson (unpubl.)
fumipennis (Burmeister)	N	N America	E	Westfall & May (1996)
immunda (Hagen)	N	N America	Min	D. Paulson (unpubl.)
lacrimans (Hagen)	N	N America	E	Westfall & May (1996)
lugens (Hagen) [2]	N	N America	0.47 (30)*	D. Paulson (unpubl.)
moesta (Hagen) [2]	N	N America	0.41 (119)*	D. Paulson (unpubl.)
nahuana Calvert	N	N America	0.08 (38)*	D. Paulson (unpubl.)
oenea Hagen in Selys [2]	N	N America	0.25 (28)*	D. Paulson (unpubl.)
pima Garrison	N	N America	Min	D. Paulson (unpubl.)
plana Calvert	N	N America	0.33 (27)*	D. Paulson (unpubl.)
sabino Garrison	N	N America	Min	D. Paulson (unpubl.)
tarascana Calvert	N	N America	Min	Westfall & May (1996)

Taxon	D	Region	Frequency	Source
Coenagrionidae: *Argia*				
tezpi Calvert	N	N America	Min	D. Paulson (unpubl.)
tibialis (Rambur) [2]	N	N America	0.19 (31)*	D. Paulson (unpubl.)
translata Hagen in Selys	N	N America	0.09 (33)*	D. Paulson (unpubl.)
vivida Hagen in Selys [3]	N	Canada	0.48-0.64 (559)	Conrad & Pritchard (1989)
		N America	0.14 (126)*	D. Paulson (unpubl.)
Ceriagrion				
aurantiacum ryukyuanum Asahina				
	P	Japan	E	Sugimura et al. (2001)
tenellum (de Villers) [3, 4, 5]	P	S France	Min	Bilek (1964)
		NW Spain	0-0.27 (3,308)	Andrés & Cordero (1999)
			0.02-0.29 (307)	Andrés et al. (2002)
		E Spain	0.75 (20)	Jödicke (1996)
		Belgium	0 (138)	Dingemanse (2000)
		Italy	0 (125)	Carini (1995)
		N Germany	0.30 (699)	Perl (1998)
		NNW Germany	0.70 (120)	R. Jödicke (unpubl.)
		NW Germany	0.98 (80)	Jödicke (2001)
		W Germany	< 0.01 (377)	Krüner (1986)
			0.03 (115)	Krüner (1989)
			0-0.06 (919)	Krüner (2003)
Chromagrion				
conditum (Hagen in Selys)	N	N America	E	Westfall & May (1996)
Coenagrion				
angulatum Walker	N	N America	Min	Walker (1953)
armatum (Charpentier)	P	Finland	Min	Valle (1927)
		England	Min	Schmidt (1929)
caerulescens (Fonscolombe)	P	Morocco	Maj	Jödicke (1995)
		Tunisia	Maj	R. Jödicke (unpubl.)
		E Spain	Maj	Jödicke (1996)
ecornutum (Selys)	P	Russia	0.07 (89)	E. Malikova (pers. comm.)
		Japan	R	Sugimura et al. (2001)
hastulatum (Charpentier)	P	Finland	R	Valle (1927)
		Germany	R	Schmidt (1929); Sternberg & Buchwald (1999)
		Norway	R	Jödicke (1986)
interrogatum (Hagen in Selys)	N	N America	Maj	Walker (1953)
johanssoni (Wallengren)	P	Finland	Maj	Valle (1927)
		E Russia	0.04 (84)	E. Malikova (pers. comm.)
lanceolatum (Selys)	P	E Russia	0.05 (225)	E. Malikova (pers. comm.)
		Japan	E	Sugimura et al. (2001)
lunulatum (Charpentier) [4]	P	Germany	R	Sternberg & Buchwald (1999)
mercuriale (Charpentier) [3, 4]	P	E Spain	Maj	Jödicke (1996)
		SW Germany	R	Sternberg & Buchwald (1999)

Taxon	D	Region	Frequency	Source
Coenagrion				
mercuriale (continued)		England	0-0.33 (2,794)	McKee et al. (2005)
ornatum (Selys)	P	SW Germany	Min, occ. Maj	Sternberg & Buchwald (1999)
puella (Linnaeus) [3, 4]	P	England	0.11 (553)	Thompson (1989)
			0.19-0.40 (271)	McKee et al. (2005)
		Ukraine	0.19 (36)	Gorb (1998)
pulchellum (Vander Linden) [4]	P	NW Europe	Min	Schmidt (1964)
resolutum (Hagen in Selys)	N	N America	E	Westfall & May (1996)
scitulum (Rambur)	P	E Spain	Maj	Jödicke (1996)
		Sardinia, Italy	Maj	B. Kunz (pers. comm.)
Enallagma				
anna Williamson	N	N America	0.32 (22)*	D. Paulson (unpubl.)
annexum (Hagen)	N	N America	0.29 (45)	Garrison (1978)
			0.51 (156)*	D. Paulson (unpubl.)
basidens Calvert	N	N America	0.11 (36)*	D. Paulson (unpubl.)
boreale Selys [3]	N	Canada	0.68 (485)	Forbes (1994)
		MI, USA	0.45 (554)	Fincke (1994)
		N America	0.67 (443)*	D. Paulson (unpubl.)
carunculatum Morse	N	N America	0.39 (139)*	D. Paulson (unpubl.)
circulatum Selys	P	Japan	E	Sugimura et al. (2001)
civile (Hagen)	N	OK, USA	0.17 (312)	Miller & Fincke (1999)
			0.29 (126)	Miller & Fincke (2004)
clausum Morse	N	N America	0.53 (40)*	D. Paulson (unpubl.)
c. cyathigerum (Charpentier) [3, 4]	P	Brandenburg, Germany	0.23 (1,261)	Beutler (1987)
		E Spain	0.76 (21)*	Jödicke (1996)
		NW Germany	0.17 (100)	Jödicke (1996)
		NNW Germany	0.67 (250)	Jödicke (unpubl.)
		Kamchatka, Russia	Min	Dumont et al. (2005)
cyathigerum risi (Schmidt)	P	Mongolia	Min - Maj	Peters (1985)
davisi Westfall	N	N America	0.41 (27)*	D. Paulson (unpubl.)
deserti Selys	P	Tunisia	Min	Jödicke et al. (2000)
doubledayi Selys	N	N America	0.23 (26)*	D. Paulson (unpubl.)
durum (Hagen)	N	N America	0.14 (42)*	D. Paulson (unpubl.)
ebrium (Hagen) [3]	N	Canada	0.07 (261)	Forbes & Teather (1994)
		MI, USA	0.15 (70)	Miller & Fincke (1999)
exsulans (Hagen)	N	N America	E	Walker (1953);
hageni (Walsh)	N	MI, USA	0.26 (370)	Fincke (1994)
			0.31 (166)	Fincke (1994)
			0.36 (103)	Fincke (1994)
minusculum Morse	N	N America	E	Westfall & May (1996)
novaehispaniae Calvert	N	N America	0.67 (36)*	D. Paulson (unpubl.)
praevarum (Hagen)	N	N America	E	Westfall & May (1996)

Taxon	D	Region	Frequency	Source
Erythromma				
lindenii (Selys) [4]	P	Europe	0	R. Jödicke (unpubl.)
		Tunisia	R	Jödicke et al. (2000)
viridulum (Charpentier) [3, 4]	P	W Germany	0.46 (194)	R. Jödicke (unpubl)
		N Germany	0.84 (117)	R. Jödicke (unpubl.)
Ischnura				
barberi Currie	N	N America	Min	D. Paulson (unpubl.)
capreolus (Hagen) [6]	N	N America	0.21 (73)*	D. Paulson (unpubl.)
cervula Selys [6]	N	N America	0.14 (172)*	D. Paulson (unpubl.)
damula Calvert [6]	N	NM USA	0.09-0.18 (1,490)	Johnson (1964)
		W Canada	R	Acorn (2004)
demorsa (Hagen) [7]	N	NM USA	0.34-0.38	Johnson (1966)
denticollis (Burmeister) [6]	N	N America	0.24 (94)*	D. Paulson (unpubl.)
		Mexico	0.51 (450)	Córdoba-Aguilar (1993)
elegans (Vander Linden) [3, 4, 7]	P	England	0.57 (164)	Parr (1965)
			0.23-0.36 (427)	Parr (1969)
			0.32 (1,048)	Parr & Palmer (1971)
		E Spain	0.29 (24)	Jödicke (1996)
		NW Spain	0.04-0.91 (528)	Sánchez-Guillén et al. (2005) [†]
	N	Ukraine	0.24 (202)	Gorb (1999)
		SW Ukraine	0.51-0.66 (183)	E. Dyatlova (pers. comm.)
erratica Calvert [6]	N	N America	0.29 (21)*	D. Paulson (unpubl.)
evansi Morton	P	Iran	E	Schmidt (1954)
fountaineae Morton [7]	P	Israel	R	Dumont (1991)
		Tunisia	R	Jödicke et al. (2000)
gemina (Kennedy)	N	CA, USA	0.01 (197)	Garrison & Hafernik (1981)
			Min	Robinson & Allgeyer (1996)
genei (Rambur) [4, 6]	P	Sardinia, Italy	Min	B. Kunz (pers. comm.)
graellsii (Rambur) [3, 4, 7]	P	NW Spain	0.01-0.40 (4,642)	Sánchez-Guillén et al. (2005) [†]
		E Spain	0.06 (50)	Jödicke (1996)
perparva McLachlan in Selys [7]	N	N America	R	Paulson (1999)
pumilio (Charpentier) [4, 7]	P	Europe	< 0.01	Seidenbusch (1995)
		S France	Min	Langenbach (1993)
		S Germany	0.15 (?)	Reiter (1993)
		NW Spain	0.16 (100)	Cordero Rivera & Andrés Abad (1999)
ramburii (Selys) [7]	N	FL, USA	0.31 (90)	Robertson (1985)
			0.39 (426)	Sirot et al. (2003)
		New World	0.23 (518)*	Paulson (unpubl.)
saharensis Aguesse [4, 6, 8]	P	Tunisia	0.15 (26)*	Jödicke et al. (2000)

Taxon	D	Region	Frequency	Source
Ischnura				
senegalensis (Rambur) [4, 6]	P	Japan	Min	M. Watanabe (pers. comm.)
		Africa, Asia	0.07 (30)*	D. Paulson (unpubl.)
verticalis (Say) [7]	N	MI, USA	0.02 (553)	Fincke (1987)
			0 (386)	Fincke (1987)
Mortonagrion				
hirosei Asahina	P	Japan	E	Sugimura et al. (2001)
Nehalennia				
irene (Hagen) [3]	N	N America	Min-Maj	D. Paulson (unpubl.)
		E Canada	0.02-0.28 (475)	Forbes et al. (1995)
			0.53 (101)	Lajeunesse & Forbes (2003)
		W Canada	Maj	Acorn (2004)
Paracercion				
c. calamorum (Ris)	P	Japan	E	Sugimura et al. (2001)
v-nigrum (Needham)	P	E Russia	0.35 (84)	E. Malikova (pers. comm.)
Pyrrhosoma				
elisabethae Schmidt [4, 9]	P	Greece	0.97 (60)	W. Lopau (pers. comm.)
nymphula (Sulzer) [4, 9]	P	S France	R	Bilek (1964)
		E Spain	Maj	Jödicke (1996)
		SW Germany	Maj	Sternberg & Buchwald (1999)
		Austria	1.00 (40)	R. Jödicke (unpubl.)
Platycnemididae: *Platycnemis*				
pennipes (Pallas)	P	Europe	R	Schmidt (1929)
Anisoptera: Aeshnidae: *Aeshna*				
affinis Vander Linden	P	S France	E	Bilek (1964)
		Germany	Min	Sternberg & Buchwald (2000)
caerulea (Ström) [10]	P	Germany	E	Sternberg & Buchwald (2000)
canadensis Walker	N	NE US & Canada	Min	Walker (1958)
clepsydra Say	N	N America	E	Dunkle (2000)
constricta Say	N	NE US & Canada	Min	P. Brunelle (pers. comm.)
crenata Hagen	P	W Siberia	Min	Petzold (2002)
cyanea (O.F. Müller) [10]	P	Europe	Min	Sternberg & Buchwald (2000)
eremita Scudder	N	N America	Min	Walker (1958)
interrupta Walker	N	N America	Min	Walker (1958)
juncea (Linnaeus) [10]	H	N America	Min	D. Paulson (unpubl.)
		NE US & Canada	Maj	P. Brunelle (pers. comm.)
		Europe	Min	Sternberg & Buchwald (2000)
		Japan	E	Sugimura et al. (2001)

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Taxon	D	Region	Frequency	Source
Aeshna				
m. mixta Latreille [3]	P	Germany	E	Schmidt (1929);
		SW Germany	Min	Sternberg & Buchwald (2000)
		E Spain	Maj	Jödicke (1996)
mixta soneharai Asahina	P	Japan	R	Sugimura et al. (2001)
nigroflava Martin	P	Japan	R	Sugimura et al. (2001)
osiliensis Mierzejewski	P	Estonia	E	Peters (1987)
palmata Hagen	N	N America	Min	D. Paulson (unpubl.)
persephone Donnelly	N	N America	E	Dunkle (2000); D. Paulson (unpubl.)
septentrionalis Burmeister	N	N America	Min	D. Paulson (unpubl.)
serrata Hagen	P	Siberia	0.46 (26)*	G. Peters (pers. comm.)
sitchensis Hagen	N	N America	Min	D. Paulson (unpubl.)
		Canada	Min	Cannings (1982)
subarctica elisabethae Djakonov	P	E Germany	Min	Peters (1987)
		E Germany	0.50 (30)	Peters (1987)
		W Germany	E	Sternberg (1995)
s. subarctica Walker	H	Canada	Min	P. Brunelle (pers. comm.)
		Japan	R	Sugimura et al. (2001)
tuberculifera Walker	N	N America	Maj	H. White (pers. comm.)
		Canada	Min	P. Brunelle (pers. comm.)
umbrosa Walker	N	N America	Min	D. Paulson (unpubl.)
verticalis Hagen	N	Canada	Min	P. Brunelle (pers. comm.)
viridis Eversmann	P	Germany	Min	Sternberg & Buchwald (2000)
walkeri Kennedy	N	N America	E	Dunkle (2000)
Anax				
junius (Drury)	N	N America	Min	Dunkle (2000)
parthenope julius Brauer	P	Japan	R	Sugimura et al. (2001)
p. parthenope Selys [4]	P	Germany	Maj	Sternberg & Buchwald (2000)
walsinghami McLachlan	N	N America	E	Dunkle (2000)
Basiaeschna				
janata (Say)	N	N America	E	Dunkle (2000)
Oplonaeschna				
armata (Hagen)	N	N America	E	Dunkle (2000)
Rhionaeschna				
californica (Calvert)	N	N America	Min	D. Paulson (unpubl.)
dugesi (Calvert)	N	N America	Min	D. Paulson (unpubl.)
multicolor (Hagen)	N	N America	Min	D. Paulson (unpubl.)
mutata (Hagen)	N	N America	R	Dunkle (2000)
Corduliidae: *Epitheca*				
costalis (Selys) [1]	N	N America	E	Dunkle (2000)
marginata (Selys) [1]	P	Japan	E	M. Watanabe (pers. comm.)

Taxon	D	Region	Frequency	Source
Libellulidae: *Crocothemis*				
erythraea (Brullé)	P	Slovenia	R	Kotarac (1996)
		Tunisia	Min	Jödicke et al. (2000)
Erythrodiplax				
berenice (Drury)	N	N America	E	Dunkle (2000)
funerea (Hagen) [1]	N	Costa Rica	0.58 (256)*	D. Paulson (unpubl.)
umbrata (Linnaeus) [1]	N	N America	0.21 (269)*	Borror (1942)
		Texas, Mexico	0.21 (187)*	D. Paulson (unpubl.)
		Central America	0.25 (60)*	D. Paulson (unpubl.)
Leucorrhinia				
dubia (Vander Linden)	P	Germany	R	Sternberg & Buchwald (2000)
glacialis Hagen	N	N America	Min	Dunkle (2000)
hudsonica (Selys)	N	N America	Min	Dunkle (2000)
proxima Calvert	N	N America	Min	Dunkle (2000)
rubicunda (Linnaeus)	P	Germany	R	Sternberg & Buchwald (2000)
Libellula				
jesseana Williamson	N	N America	Min	Dunkle (2000)
Perithemis				
tenera (Say) [1]	N	N America	R	H. White (pers. comm.)

[1] Polymorphism in wing coloration.
[2] Polymorphic but without real andromorph; in these cases, andromorph frequency refers to the most male-like morph.
[3] Exhibits significant inter-populational differences in morph frequency.
[4] More than two mature color morphs with at least one real andromorph.
[5] Only f. *erythrogastrum* is considered under „Frequency" but also f. *intermedium* and f. *typicum* may be assigned to andromorphs.
[6] Developmental morph, copulation not recorded.
[7] Developmental morph, copulation recorded.
[8] Andromorphs are green like the males; blue females also occur but were scored as heteromorphs.
[9] Both f. *typicum* and f. *fulvipes* are assigned to andromorphs.
[10] In breeding experiments, andromorph frequency rises with higher temperature (Sternberg 1995).
[11] Females exhibit continuous variation in color that may represent intermediates in post-teneral color development [only Table 3].

Of the 109 polymorphic species for which we compiled some information of andromorph frequency, this morph was the majority morph in at least one population in 17% of the polymorphic species. In one case (*I. denticollis*), the reported morph frequencies did not differ from equality. Despite a paucity of frequency data for most genera, the minimum andromorph frequency was significantly higher for *Enallagma* ($\bar{x}$ = 0.30 ± 0.05, n = 14) than for *Ischnura* ($\bar{x}$ = 0.15 ± 0.04, n = 12), even after excluding the two polymorphic, monogamous *Ischnura* species, which only rarely had andromorphs (t = 2.41, p = 0.02). There were sufficient quantitative data on morph frequencies to demonstrate significant differences across populations of 11 species; for an additional six species, andromorphs represented a minority in at least one population but the majority morph in another. The extreme case was exemplified by *Nehalennia irene*, which was primarily andromorphic in the western part of its range and primarily heteromorphic in the eastern part (Table 2).

DISCUSSION

Our results have broad implications for the study of sexual conflict more generally, particularly because variation in female signaling is often not as obvious as it is in Odonata with female-specific color polymorphisms. For example, if blue coloration is ancestral within the *Enallagma* clade, then sexual dimorphism in color patterns would presumably have resulted from sexual conflict of interest, rather than sexual selection. On the other hand, among the *Ischnura* species surveyed, only two were monomorphically andromorphic. Several *Ischnura* species (*demorsa, hastata, kellicotti, perparva, posita, verticalis*) with monogamous females (Fincke 1987; Robinson & Allgeyer 1996) have evolved that condition independently (Fig. 3). Because such females consistently refuse to mate unless they lack sperm, both females and males should benefit from females being sexually dimorphic in their coloration and hence, obvious to males. Interestingly, the only two polymorphic monogamous species are those in which the andromorphs are so rare as to make the species effectively monomorphic (Table 2). Determining whether the state of monomorphy in *Enallagma* species is adaptive or the result of evolutionary history remains a challenge. In *Enallagma*, if the andromorph is homozygous recessive and heteromorphs result from a dominant gene, then heteromorphs could rapidly become the majority morph type when polymorphism is favored. Work on the inheritance of color in *Enallagma* is currently underway.

The blue colors that are common among male coenagrionids and other Odonata are structural, resulting from coherent light scattering from nanostructures within the integument. The source of blue colors in male *E. civile* and the anisopteran *Anax junius* was identified as an array of nanospheres in the epidermal cells immediately below the cuticle (Prum et al. 2004). It would be parsimonious to infer that blue female andromorphs possess similar cuticular ultrastructures that are the primitive condition for the genus *Enallagma*. The source of color in female heteromorphs is unknown but may simply involve the absence of the nanosphere arrays from epidermal cells or the shielding of blue structural colors by absorptive pigments distal to the arrays. The females of some polymorphic species such as *E. civile* exhibit a partial expression of structural blues on some body segments (Miller & Fincke 1999, see also Forbes 1994). The yellow, orange and red colors of several *Enallagma* species result from pigments that have yet to be identified chemically.

Table 3. Monomorphic species within the two major families of mate-searching Odonata that include polymorphic species — A: andromorphic; H: heteromorphic – with respect to the general morph type of mature females. Key to superscripts and further abbreviations are the same as in Table 2. Species whose female morph types are still insufficiently studied are omitted.

Taxon	D	Type	Reference
Coenagrionidae			
Argia agrioides Calvert	N	H	Westfall & May (1996)
bipunctulata (Hagen)	N	H	Dunkle (1990)
hinei Kennedy	N	H	Westfall & May (1996)
leonorae Garrison	N	H	D. Paulson (unpubl.)
munda Calvert	N	H	D. Paulson (unpubl.)
pallens Calvert	N	A	Westfall & May (1996)
rhoadsi Calvert	N	H	Westfall & May (1996)
sedula (Hagen)	N	H	Dunkle (1990)
tonto Hagen	N	H	D. Paulson (unpubl.)
Ceriagrion melanurum Selys	P	A	Sugimura et al. (2001)
nipponicum Asahina	P	H	Sugimura et al. (2001)
Coenagrion hylas freyi (Bilek)	P	H	R. Jödicke (unpubl.)
h. hylas (Trybom)	P	H	Sugimura et al. (2001)
intermedium Lohmann	P	H	Jödicke (2005)
terue (Asahina)	P	A	Sugimura et al. (2001)
Enallagma antennatum (Say)	N	A	Westfall & May (1996); Lam (2004)
aspersum (Hagen)	N	A	Fincke & Miller (2004); Lam (2004)
coecum (Hagen)	N	A	Dunkle (1990)
concisum Williamson [6]	N	H	Dunkle (1990)
daeckii (Calvert)	N	A	Dunkle (1990)
divagans Selys	N	A	Dunkle (1990)
dubium Root	N	H	Dunkle (1990)
geminatum Kellicott	N	A	Westfall & May (1996)
laterale Morse	N	H	Lam (2004)
pallidum Root	N	A	Dunkle (1990)
pictum Morse	N	H	Westfall & May (1996)
pollutum (Hagen) [6, 11]	N	A	Dunkle (1990)
recurvatum Davis	N	H	Lam (2004)
semicirculare Selys	N	A	Westfall & May (1996)
signatum (Hagen) [7, 11]	N	A	Tennessen (1975)
sulcatum Williamson [6, 11]	N	A	Dunkle (1990)
traviatum Selys	N	A	D. Paulson (unpubl.)
vesperum Calvert [6, 11]	N	A	D. Paulson (unpubl.)
weewa Byers	N	A	Lam (2004)
Erythromma humerale Selys	P	H	Sugimura et al. (2001)
najas (Hansemann)	P	H	Schmidt (1929)
Ischnura aralensis Haritonov [6]	P	A	Haritonov (1988)
asiatica Brauer [6]	P	H	Schmidt (1954); Sugimura et al (2001)
aurora Brauer	P	H	Schmidt (1954); Sugimura et al (2001)
forcipata Morton [6]	P	H	Schmidt (1954)
hastata (Say) [7]	N	H	Robinson & Allgeyer 1996

Taxon	D	Type	Reference
kellicotti Williamson [7]	N	A	D. Paulson (unpubl.)
posita (Hagen) [7]	N	H	Robinson & Allgeyer 1996; Lam (2004)
prognata (Hagen) [6]	N	H	Dunkle (1990); Lam (2004)
Mortonagrion selenion (Ris) [6]	P	H	Sugimura et al. (2001)
Nehalennia gracilis Morse	N	A	Dunkle (1990)
integricollis Calvert	N	H	Dunkle (1990)
pallidula Calvert	N	A	Dunkle (1990)
speciosa (Charpentier) [6]	P	H	Schiess (1973); Naraoka (2003)
Paracercion hieroglyphicum (Brauer)	P	H	Sugimura et al. (2001)
plagiosum (Needham)	P	H	Sugimura et al. (2001)
sexlineatum (Selys)	P	H	Sugimura et al. (2001)
sieboldii (Selys)	P	H	Sugimura et al. (2001)
Aeshnidae			
Aeshna grandis (Linnaeus)	P	A	Schmidt (1929)
Anax ephippiger (Burmeister)	P	H	Schmidt (1929); Sugimura et al. (2001)
guttatus (Burmeister)	P	A	Sugimura et al. (2001)
immaculifrons Rambur	P	A	D. Paulson (unpubl.)
imperator Leach [6]	P	A	Corbet (1957)
longipes Hagen	N	H	Dunkle (2000)
n. nigrofasciatus Oguma	P	H	Sugimura et al. (2001)
Rhionaeschna psilus (Calvert)	N	H	D. Paulson (unpubl.)

The observation that males of some species in the subclade including *E. signatum* exhibit a blue phase (Lam 2004) prior to developing a yellow or red coloration at maturity suggests that pigments form in the integument distal to a nanosphere array that is plesiomorphic for the group. Females in the *E. signatum* clade also exhibit long-wavelength colors, but they are less bright and saturated than those of the males owing perhaps to lower densities of pigment. Tenerals of both sexes in this clade are blue, and some mature females exhibit a blue-green to yellow-green hue that may result from a mix of yellow pigments and a structural blue resulting from a nanosphere array. Taken together, these observations imply that the integumentary structure responsible for blue colors in *Enallagma*, and hence female andromorphs, is plesiomorphic for the genus. However, the blue colors of juvenile males and females in the *signatum* clade of North American *Enallagma* may have a pigmentary rather than structural origin (T. Schultz unpubl.).

In European *Coenagrion*, and north American *Argia*, similar to the blue clades of *Enallagma*, most males are at first a pale gray-blue before becoming blue at maturity. However, in *Ischnura*, some males are blue (e.g. *kellicotti*), whereas others have green thoraxes at sexual maturity. In *I. ramburii*, a species basal to a major clade (Fig. 3), young andromorphs are blue before becoming male-like with green thoraxes (Sirot et al. 2003). In *I. saharensis*, the males are green, but a blue female morph occurs in addition to the vividly green andromorph (Jödicke et al. 2000). In *I. elegans, I. graellsii*, and *I. pumilio*, males are first green before turning blue at maturity (resp., Parr & Palmer 1971; Cordero Rivera 1987; Brooks & Lewington 1999). Understanding the evolution of male, and andromorphic female,
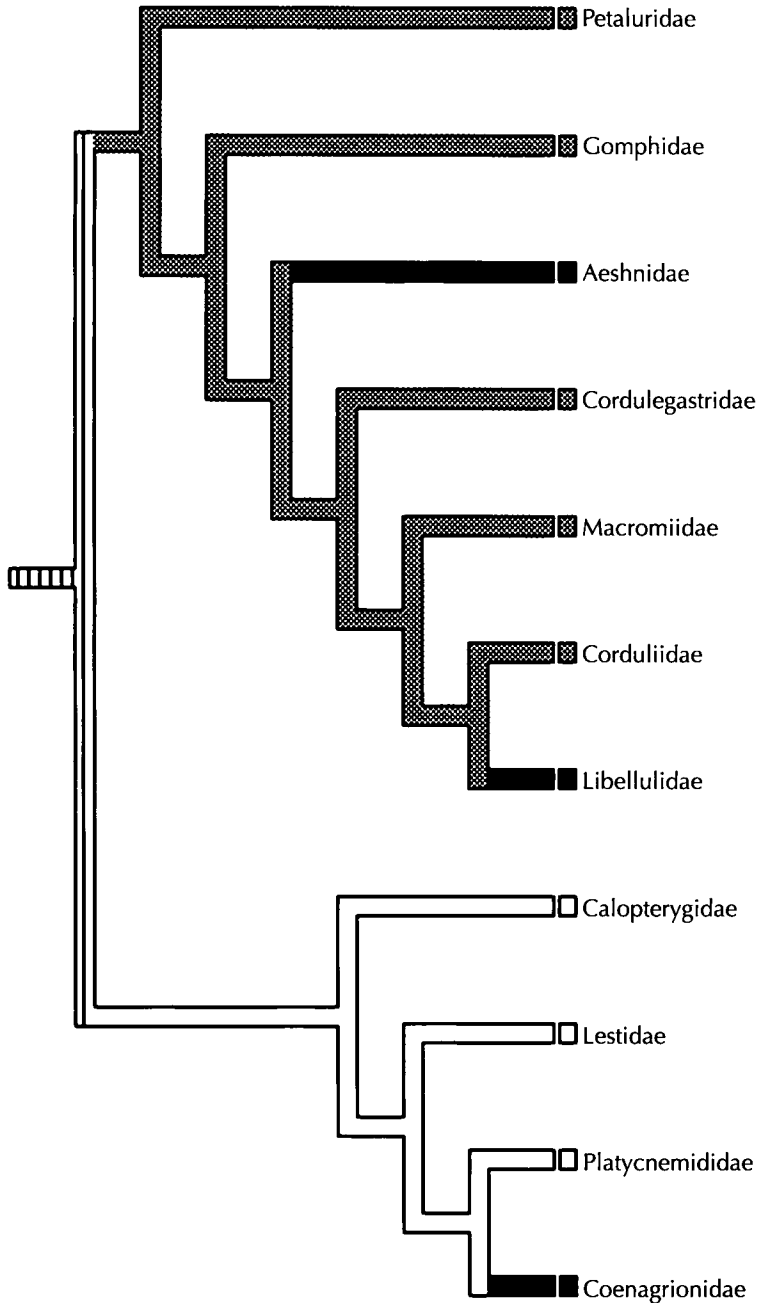
Figure 2: Color state mapped onto morphological phylogeny of Rehn (2003) indicates that female-specific color polymorphisms have evolved independently at least three times. — Gray: primarily sexually monochromatic; White: primarily sexually dichromatic, female polymorphism rare; Black: primarily sexually dichromatic, female polymorphism common; Stripes: equivocal.

coloration will require molecular phylogenies for *Argia*, *Coenagrion*, and European *Ischnura*. Although developmental variation may be a pre-adaptation for the evolution of genetic color polymorphism, our categorization of *Ischnura* species based on the female developmental color pattern and type of polymorphism did not represent North American clades according to the phylogeny of Chippendale et al. (1999). This suggests either little phylogenetic constraint in the developmental pathways for the color polymorphism, or that the phylogeny may need to be re-examined in light of the great similarities among certain species they considered in different clades.

The observed variation among species in female signals was more consistent with the LMR hypothesis than with any mimicry-based model. Many polymorphic species effectively have more than two morphs, and several species are polymorphic but lack andromorphs altogether. In the latter cases, it is the male that has diverged from a blue ancestral state. In a few cases, andromorphs resemble congeneric, but not conspecific, males. This would be consistent with the assumptions of male mimicry only if congeneric harassment were greater than conspecific harassment. Even though none of the above constitute a test of the LMR hypothesis, all of the results were at least consistent with the LMR assumption that such variation makes it more difficult for a male to cue to any specific female type. Although andromorphs were usually the minority morph, they represented the most common female type in populations of 17% of the species for which we had some frequency data. Measuring male reactions to females in such populations would offer a ready test of alternative hypotheses. Sherratt's (2001) model predicts that even when andromorphs are in the majority, male morph preference for andromorphs should never exceed their preference for heteromorphs. On the other hand, the LMR hypothesis predicts that males should respond sexually more often to the majority morph, regardless of morph type.

In light of the large number of species and populations in which all or most of the females present are male-like, and hence "typical", the recent trend among authors (e.g. van Gossum et al. 2001a; Sherratt & Forbes 2001) to replace Johnson's (1975) descriptor 'hetero' with 'gyno' (i.e. gynochromatype, Hilton 1987; Corbet 1999; gynomorph, Paulson 1999) seems ill-advised. We advocate Johnson's terminology of heteromorph to designate types that differ from male coloration, or even a series of more descriptive names when there are multiple types, as Parr (1999) suggested. All females possess female-specific traits which males might potentially use for sexual recognition, though they are more obvious in some species than others. Many female coenagrionids differ from males in having a lighter pterostigma on the otherwise clear wings and a different pattern of black pigmentation on the abdomen. In several monomorphic species, the sexes differ in the size and/or the color of their postocular spots. For example, in *E. aspersum*, female andromorphs in some populations have green postocular spots, whereas in the male they are blue (O. Fincke unpubl.).

Several monomorphic species are functionally polymorphic (Table 3), whereas developmental morphs functionally increase the number of morphs in polymorphic species. To the extent such females mate, they add to the number of female variants, and, according to the LMR, to male confusion. More attention needs to be given to the behavior and color development of these female variants. For example, when
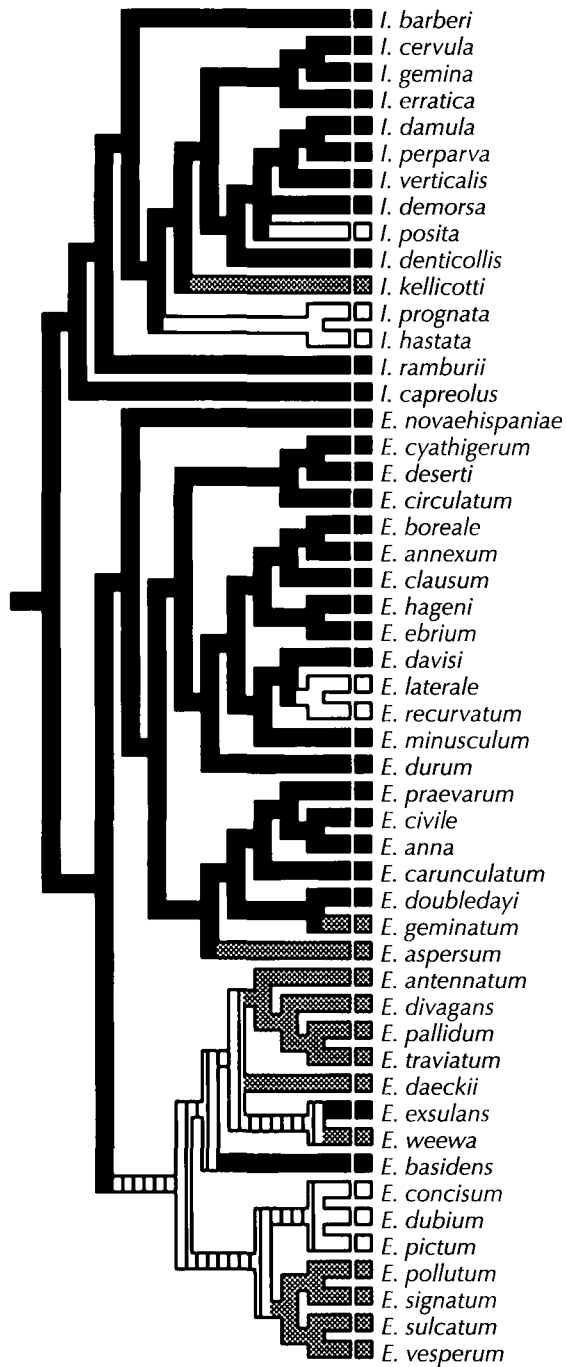
Figure 3: Color variants mapped on current phylogenies for *Enallagma* (after Turgeon et al. 2005) and *Ischnura* (after Chippendale et al. 1999). — White: heteromorphs only, Gray: andromorphs only; Black: polymorphic, Stripes: equivocal.

the developmental color morph was included in the analysis, the mating patterns of *I. ramburii* in the study by Sirot et al. (2003) supported the LMR hypothesis, despite the authors' final conclusion that their data were more consistent with Sherratt's (2001) model. In *Enallagma* species such as *E. civile*, which lack a distinct developmental morph, both morph types exhibit a continuum of color variation during development. Because such females are known to mate (T. Schultz unpubl.), males may attend to a much greater range of female phenotypes than is represented by genetically controlled morph types, assuming that they can perceive such differences. Our conclusions concur with Corbet's (1999) admonition against equating polychromatism resulting from age and/or environmental effects with genetic polymorphism.

We found tentative support that andromorphs are more likely to have a lower frequency in *Ischnura* than in *Enallagma* species. However, the assumption that *Ischnura* andromorphs are more apparent than those of *Enallagma* needs to be tested using quantitative data on vector distance between male and female signals. We also lack data on the type and number of co-occurring congeneric species, as well as signal/noise ratios of morph types, which may additionally affect a male's ability to recognize females as potential mates. In our experience, North American *Enallagma* species are much more likely to co-occur with similar congeners than are *Ischnura* species, which co-occur commonly in Europe. Males of many *Enallagma* species contribute to per capita harassment rate by responding sexually to congeneric females (e.g. Paulson 1974; Miller & Fincke 2004; O. Fincke and A. Farge-vieille unpubl.). Across populations of a given species, morph frequencies often varied significantly as expected if equilibrium frequencies of the same species differ as the result of variable morph-environment interactions (see Fincke 2004).

Crypsis of a morph may vary across a species' range because of differences in background vegetation, environmental effects on the development of color patterns or co-occurring species. Quantification of morph frequency, signal apparency of both sexes using radiospectrometry, per capita harassment, and density is underway (T. Schultz & O. Fincke), and should provide a picture of how these variables co-vary across populations and species, offering more rigorous tests of the underlying patterns suggested here. Further study of species with andromorphs as the majority morph in some populations, but the minority morph in others (e.g. *Nehalennia irene*, *Ischnura elegans*, and *Lestes sponsa*), should offer particularly fruitful insights into factors responsible for the variation in morph frequencies across a species' range.

Female color polymorphisms are known in tropical species (e.g. Paulson 1998; McKee et al. 2005) but, in our experience, are uncommon. For example, in Costa Rica, all species of *Argia*, a genus whose distribution spans the Nearctic-Neotropical divide, are monomorphic (D. Paulson pers. obs.). This trend is expected if female polymorphism functions to reduce sexual harassment. The lower density of many tropical populations should produce less sexual harassment than is found in the higher densities that characterize many Holarctic polymorphic species. To test this and other hypotheses presented herein, we urge field researchers to pay more attention to female signal variation in the Odonata, and where polymorphisms occur, to note morph frequency within and between populations.

Acknowledgements

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